BIOLOGY AND REPRODUCTION OF SOME AUSTRALIAN SPECIES OF MACROCHELIDAE (ACARINA)

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Abstract

The relationship between distribution and reproductive behaviour was examined in Australian species of Macrochelidae. Species that reproduce by thelytokous parthenogenesis (*Macrocheles penicilliger*, *M. peniculatus*, *M. virgo*) were usually found in temporally stable, physically continuous habitats such as leaf litter and compost. Sexually reproducing (arrhenotokous) species (*M. glaber*, *M. subbadius*, *M. merdarius*, *M. robustulus*, *Glyptholaspis americana*) were found in a variety of habitats, but especially in ephemeral scattered habitats (dung pads in pasture). It has been argued that thelytokous species should have an advantage in colonising patchy disturbed habitats, but the females of arrhenotokous macrochelids are able to mate with their sons, and are commonly phoretic on insects. These factors make them effective colonisers of new or disturbed habitats.

Introduction

Mites of the family Macrochelidae are common inhabitants of all kinds of decomposing organic matter, including leaf litter, compost, and dung. It has been suggested that there is a clear ecological distinction between macrochelid species occurring in two different types of habitat. Some species, including the *Macrocheles glaber* group, occur in transient, spatially scattered habitats such as isolated dung pads in pasture. Others occur in spatially continuous and temporally predictable habitats such as natural leaf litter (e.g. the genus *Geholaspis*) or in spatially restricted but still temporally predictable habitats, such large dung accumulations (e.g. *Macrocheles muscaedomesticae*) (Krantz 1983; Hyatt and Emberson 1988). Occurrence in these two types of habitat may have different implications for the life cycle, behaviour, and reproductive mode of the species concerned. The genus *Macrocheles* offers an opportunity to examine these phenomena, since it occurs in all of these types of habitat, and includes both obligate thelytokous species and species with sexual reproduction (Filipponi 1964). Macrochelids have some advantages as experimental animals, such as small body size (1 mm or less) and short generation times (ca. 1 week). We have therefore examined some Australian species of Macrochelidae, and compared their modes of reproduction, habitat preferences, and colonising ability.

Materials and Methods

The mites used in this study were collected by MJM from January to August 1991, from the following localities: *Glyptholaspis americana* (Berlese), Frankston, Victoria, leaf litter and compost (94 females); Hampton, Victoria, compost (1 female); Melbourne, Victoria, compost (1 female); Mount Eliza, Victoria, compost (3 females); Fyshwick, ACT, cattle dung at dairy (2 females); *Macrocheles glaber* (Müller), Langwarrin, Victoria, dung in pasture (5 females); Fyshwick, ACT, cattle dung at dairy (8 females); Hampton, Victoria, compost (8 females); *Macrocheles penicilliger* (Berlese), Mount

Eliza, Victoria, leaf litter and compost (ca 700 females); Frankston, Victoria, leaf litter (20 females); *Macrocheles peniculatus* Berlese, Monash University, Victoria, sawdust in aviary (8 females); Leongatha, Victoria, dung in milking yard (2 females); *Macrocheles merdarius* (Berlese), Fyshwick, ACT, cattle dung at dairy (3 females); *Macrocheles virgo* Halliday, Cairns, Queensland, leaf litter (12 females); *Macrocheles subbadius* (Berlese), Mount Eliza, Victoria, compost (1 female); *Macrocheles robustulus* (Berlese), Fyshwick, ACT, dung at dairy (2 females). Mites were identified according to the criteria of Halliday (1986a, 1986b, 1993) and Hyatt and Emberson (1988).

Mites were extracted from their substrates using a Tullgren funnel, or were collected individually in the field using an aspirator or a fine brush. Mites were reared in plastic specimen tubes with a plaster/charcoal floor (Walter and Ikonen 1989). Cages were kept at 26°C in plastic boxes with moist paper to maintain high humidity. Individual mites were removed from these cages at the protonymph stage and reared to adult in isolation, to ensure their virginity. Food was provided every 24 hours. All species were successfully reared and completed their development on a diet of the eggs of *Lucilia* sp., *Musca vetustissima* Walker (Diptera), or nematodes (*Panagreilus* sp.). Fly eggs used as food were frozen for preservation and to prevent them from hatching. All mite species would sometimes feed on mite prey (*Zygoseius*, *Lasioseius*), but would not attack Collembola or oribatid mites.

Results

Collection records

This study presents the first record of *Macrocheles penicilliger* from Australia, and the first record of *Glyptholaspis americana* from Victoria. Failure to record these species previously may be attributed to the fact that most published records of Australian Macrochelidae have been drawn from pasture dung and dung beetles, with relatively little attention having been paid to the compost habitats in which these two species commonly occur.

Mode of reproduction

All mite species produced progeny without mating. Virgin females of *G. americana* (9 parent females) and *M. glaber* (13 parent females) produced only male progeny, indicating reproduction by arrhenotokous parthenogenesis. Virgin females of *M. penicilliger* (8 parent females), *M. peniculatus* (20 parent females), and *M. virgo* (22 parent females) produced only female progeny, indicating reproduction by thelytokous parthenogenesis. In cultures of *M. virgo*, 71 adult females were produced over 6 generations without the production of a single male. These results for *G. americana*, *M. glaber*, *M. peniculatus*, and *M. penicilliger* are consistent with previous findings (Filipponi 1964). Bregetova and Koroleva (1960) reported males of "*M. penicilliger*", but these specimens were subsequently shown to belong to a different species, *M. minervae* (Cicolani 1983). The thelytokous species *M. virgo* is morphologically very similar to *M. faveolus* Halliday, in which males

are known to occur (Halliday 1993). This situation parallels the relationship between the arrhenotokous species *M. muscaedomesticae* (Scopoli) and its thelytokous sibling species *M. similis* Krantz and Filipponi (Halliday 1990).

Mother-son matings were attempted for *G. americana* and *M. glaber*. In both cases males were seen to ride on the back of their previously unmated female parent, and in both species female progeny were sometimes produced from these matings, indicating that fertilisation had taken place (1 case out of 4, and 3 cases out of 10, respectively).

Habitat preference

The species in this study may be divided roughly into those that occur in transient scattered habitats (dung pads in pasture), and those that occur in continuous habitats (leaf litter, compost, dung accumulations). They may also be classified by whether or not they are commonly phoretic on insects, based on the data of Wallace (1986) and subsequent observations (Table 1). *Glyptholaspis americana*, *Macrocheles glaber*, *M. subbadius*, and *M. merdarius* may easily be collected in large numbers while phoretically attached to dung beetles, or, more rarely, other dung-breeding insects. *M. peniculatus* and *M. robustulus* are rarely collected in this way, even when they are abundant in the surrounding habitat. *M. penicilliger* and *M. virgo* have never been collected on insect carriers in Australia, although *M. penicilliger* may occasionally be found on *Trox scaber* in Britain (Hyatt and Emberson 1988).

M. peniculatus, *M. virgo*, *M. penicilliger* and *M. subbadius* were found only in stable or continuous habitats, *M. merdarius* and *M. robustulus* were found only in dung pads in pasture, while *M. glaber* and *G. americana* occurred in both habitat types. Other studies have shown similar patterns of distribution

Table 1. Habitat preferences, reproductive mode and occurrence of phoresy in Australian Macrochelidae.

* T = thelytokous, A = arrhenotokous

Species	Reproductive* mode	Phoresy	Temporary habitats	Continuous habitats
M. penicilliger	T	no		leaf litter, compost
M. virgo	T	no		leaf litter
M. peniculatus	T	rare		aviary, milking yard
G. americana	A	yes	pasture dung	leaf litter, compost
M. glaber	A	yes	pasture dung	compost
M. subbadius	A	yes		compost
M. merdarius	A	yes	pasture dung	
M. robustulus	A	rare	pasture dung	

for these species, with the addition that *M. peniculatus* may be found in pasture dung as well as dung accumulations (Krantz 1983; Wallace 1986).

A survey of other Australian species of Macrochelidae yielded similar results. The fauna includes a total of 28 species that can be clearly classified as typical of either continuous or discrete habitats, and whose mode of reproduction has been established (including 9 undescribed species of *Macrocheles*). Of these 28 species, 12 are typical of permanent habitats (3 thelytokous, 9 arrhenotokous) and 16 are typically found in isolated dung pads in pasture (1 thelytokous, 15 arrhenotokous) (Halliday 1986a, 1986b, 1988, 1990; Wallace 1986; and new data). Thelytokous species do not occur preferentially in temporary habitats (2x2 contingency table, exact probability 17.2%). It should be pointed out that "arrhenotoky" is here interpreted loosely, to mean that the species includes both males and females. In most cases haplodiploidy has not been rigorously proved.

Discussion

Hyatt and Emberson (1988) classified *Macrocheles* into "Leaf-litter species", "Coprophilic species" and "Intermediate species". Five species are included in both that study and the data presented here. We agree in classifying *M. robustulus*, *M. glaber*, and *M. merdarius* as coprophilic, occurring in isolated dung pads. Hyatt and Emberson classified *M. subbadius* as coprophilic, but it appears to be more ecologically flexible than that would suggest. The single female collected in this study came from a compost heap, but the ANIC contains specimens of this species from dung pads, phoretic on sepsid flies, in leaf litter, in a large dung pile at stables, and in dung-baited pitfall traps. Hyatt and Emberson classified *M. penicilliger* as "Intermediate", on the basis of morphological criteria, but their ecological data for this species agree with ours in showing that this is a species typical of leaf litter and similar predictable habitats.

Bell (1988) suggested that parthenogenetic (ie., thelytokous) animals are inferior competitors in most habitats, but since each thelytokous female could potentially found a colony, they should be good colonists, and should tend to occur preferentially in recent, novel, or disturbed environments in which competition is reduced. The species included in this study do not follow this trend. The thelytokous species studied here usually occurred in spatially continuous and temporally predictable habitats such as leaf litter, compost, and dung accumulations, and were absent from ephemeral dung pads. The sexually reproducing species occurred in a variety of habitats, but especially in physically isolated transient habitats, as represented by isolated dung pads in pasture. This observation may be partly explained by the pattern of mating behaviour employed by these dung-pad inhabiting species. If, as seems likely, females of arrhenotokous species are mated before they begin a colonising attempt, they will arrive in a novel habitat fully prepared to found a new population. Even if a colonising female has not been mated, she is able to produce male progeny from unfertilised eggs, and then mate with her sons to

produce a viable bisexual population. The frequency of mother-son matings under natural conditions is not known, and may be limited if females become unreceptive as they age (Filipponi and Ilardi 1959). Nevertheless, the opportunity for such matings may mean that thelytokous species have no advantage in colonising ability over their arrhenotokous relatives arising from this cause. Furthermore, the arrhenotokous species are commonly phoretic on insects, and consistently bear a bidentate tooth on the movable digit of the chelicera, which is used for attachment to their host (Walter 1984). The thelytokous species lack this tooth and are rarely phoretic, and their inability to disperse in this way may reduce their ability to colonise temporary habitats.

The same trend may be seen in other macrochelids that were not included in this study. The genus *Geholaspis* Berlese occurs in soil and accumulations of organic matter, is not phoretic, but is completely thelytokous (Filipponi 1964), and the occasional reports of males in this genus have subsequently been discredited. Other non-phoretic soil dwelling species such as *Macrocheles terreus* (Berlese) and *M. montanus* (Willmann) are also thelytokous (Filipponi 1964). Males of some of these species have been seen on rare occasions, but thelytoky remains their principal means of reproduction. *M. similis* Krantz and Filipponi may represent an interesting exception to this pattern. Australian populations of this species are both thelytokous and phoretic, and occur in isolated dung pads in pasture. However, the females retain a fully-developed spermathecal apparatus, suggesting that thelytoky in this species is of recent evolutionary origin (Halliday 1990). Apparently normal spermathecae have been reported in thelytokous species in other genera, such as *Lasioseius* Berlese (Walter and Lindquist 1989) and *Geholaspis* Berlese (Athias-Henriot 1968).

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